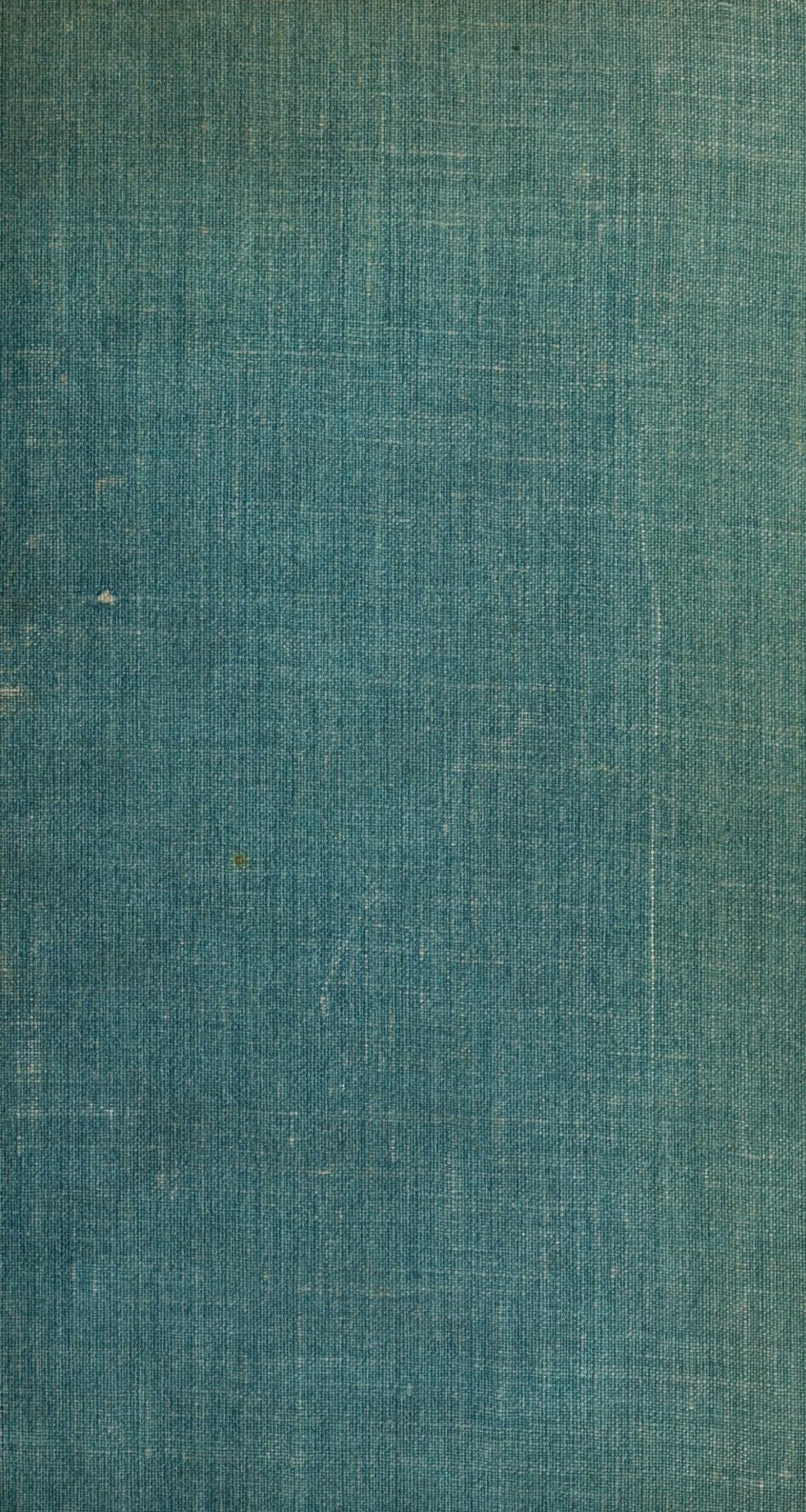






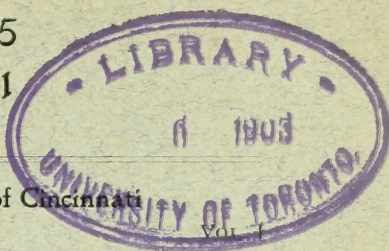


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# UNIVERSITY OF CINCINNATI

Bulletin No. 5

November, 1901

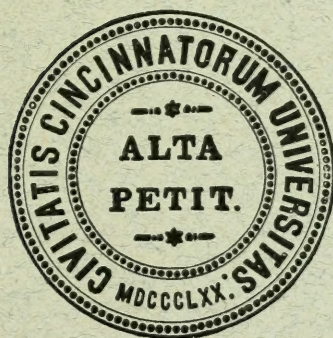


Publications of the University of Cincinnati

SERIES II.

## An Investigation of the Vascular System of *Bdellostoma dombeyi*—

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The University Bulletins are Issued Quarterly

Entered at the Post Office at Cincinnati, Ohio, as second-class matter

UNIVERSITY PRESS

Cincinnati, Ohio





AN INVESTIGATION OF THE VASCULAR SYSTEM  
OF BDELLOSTOMA DOMBEYI.

The *Cyclostomata* derive their interest and importance from the fact that they are not only the lowest of the *Craniata*, but also possess many structural features which are undoubtedly ancestral in their character. As Dr. Ayers has maintained, too little attention has been paid to this class, especially to the Myxinoid division. With the exception of Johannes Müller's "Vergleichende Anatomie der Myxinoiden" (published 1834-1842), the Myxinoids, especially *Bdellostoma*, have scarcely been touched. A closer examination of the anatomy of the blood-vascular system of *Bdellostoma*, and a discussion of a few points concerning its comparative anatomy in the light of our present knowledge, is the purpose of this paper.

The material used in the following investigation included several injected specimens, and a large number of uninjected specimens of *Bdellostoma dombeyi* collected by me during the summer of 1897, in the Bay of Monterey, at Pacific Grove, California. Carmine-gelatine was used for injection, and the specimens were preserved in alcohol-formalin mixture (95 per cent alcohol, 6 parts; 2 per cent formalin, 4 parts). For comparison I have used specimens of *Bdellostoma forsteri* (from the Cape of Good Hope), *Petromyzon*, *Myxine*, etc., belonging to Dr. Ayers, under whose direction the following investigation was made.

## THE HEART.

(Figures I, II, III, also, IX, X, XIV).

The heart is composed of three chambers — sinus venosus, auricle, and ventricle.

The *sinus venosus* (Figs. I, II, S), (gemeinschaftlichen Körperpervenienstamm of Müller), is that part of the heart which



receives the blood from the venous system. It is an elongated thin-walled sac, about 2 cm. in length, situated a little to the left of the median line, just above the anterior lobe of the liver, and between the sheets of mesentery which form the hepatic ligament. The larger posterior portion lies just below the alimentary canal, and anterior to the gall cyst. The smaller anterior portion lies beneath the auricle (A). The sinus lies outside the pericardial cavity, but is partially enclosed between the layers of the mesocardium. It is dilated posteriorly, being somewhat quadrilateral in outline, and compressed laterally. In this region the sinus receives, on the right side, the anterior and posterior hepatic veins (ha, hp). At the posterior extremity it receives the posterior common cardinal trunk (pcc). Anteriorly, it receives, on the left side, the left anterior cardinal vein (acl). The narrow anterior portion of the sinus venosus receives the inferior jugular vein (jv) just anterior to the sinu-auricular aperture, which lies in the dorsal wall near the anterior end.

The *auricle* (Figs. I, II, III, A) lies immediately above and anterior to the sinus. It occupies the left portion of the pericardial cavity, and is surrounded by the pericardium (its relations to which will be described in detail later). The auricle is the largest of the cardiac divisions, and, when expanded, almost completely fills the left pericardial cavity. When contracted, however, it is smaller than the ventricle, since it is very thin-walled. It is an elongated sac, irregular in shape, and flattened dorso-ventrally. The exact position and extent varies considerably in different specimens. It is somewhat irregularly convex, except the inner and upper walls. These are usually concave, on account of being closely apposed to the ventricle during life. The auricle usually lies for the most part on the left side of the alimentary canal. Posteriorly, the auricle is closely connected ventrally with the sinus, communicating with it through the sinu-auricular aperture. On the right side it communicates with the ventricle through a short canal, the *ductus auricularis*. (See Figs. I and II.) This duct, though well marked in some specimens, is obscured in others by the approximation of the auricular and ventricular walls. It is really a constricted portion of the auricle at the auriculo-ventricular aperture. The margin of the auricle

behind this duct usually projects as a lateral pocket into the right pericardial cavity. The auricle is attached ventrally and internally (*i. e.*, to the left) by the mesocardium. The anterior and posterior extremities of the auricle, however, project freely into the over-lying pericardial cavity.

The cavity of the auricle (Fig. III) is very irregular. Beside the three pocket-like spaces (anterior, posterior, and lateral), the cavity is made irregular by a network of muscular trabeculæ which project from the walls, and sometimes across the cavity. The auricle has two openings. The afferent, or sinu-auricular aperture, is in the posterior portion of the floor. On viewing the floor from above, the long narrow slit-like opening is seen extending diagonally from side to side. The opening is guarded by two thin membranous valves (Fig. III, sav), whose free margins readily allow the influx of blood, but effectually prohibit its reflux. A short distance anterior from the sinu-auricular opening we find the auriculo-ventricular aperture, an oval foramen, on the right side in the duct previously described. This aperture is also guarded by a pair of valves, semi-lunar in shape, one lying anterior and the other posterior to the opening. These valves are smaller but stronger than the sinu-auricular valves. During the flow of blood from the auricle into the ventricle they lie flattened against the sides of the duct, with their free margins extending toward the ventricle and offering no resistance to the flow of blood. During the ventricular systole the valves prevent the reflux of blood by the apposition of their free margins in the median line, completely closing the channel.

The *ventricle* (Figs. I, II, III, V) is an ovoidal sac, slightly elongated and flattened dorso-ventrally. The lateral margin on the left side, next to the auricle, is less convex than that on the right. The ventricle is nearly in the median line of the body, just below the alimentary canal. It lies to the right of the auricle, somewhat ventral and anterior to it. The wall of the ventricle is much thicker than that of the auricle, and encloses a cavity shaped like a Scottish bag-pipe (See Fig. III). The inner surface of the wall, like that of the auricle, is marked by projecting muscular trabeculæ. There are two openings into the ventricular cavity. The afferent,



or auriculo-ventricular is an oval foramen situated near the posterior end on the inner side. It corresponds to the end of the short ductus auricularis already described. The foramen ordinarily measures about a millimeter in diameter in individuals of fifty centimeters length. The afferent or aortic aperture lies at the anterior extremity of the ventricle. It is nearly circular in outline and is likewise guarded by a pair of strong semi-lunar valves, one dorsal and one ventral. These are the strongest and thickest of the cardiac valves. They contain much elastic tissue, and are continuous with the walls of the aorta at its base. Their action is similar to that of other valves.

#### PERICARDIAL CAVITY.

The alimentary canal in *Bdellostoma* is suspended from the mid-dorsal line of the body wall by a mesentery, which is formed by the reflection of the lateral peritoneal sheets. (See Fig. IV., m.). Ventral to the alimentary canal, in the anterior abdominal region, the liver is likewise enclosed by a continuation of the same mesentery. (See Fig. V, L). Above the anterior lobe of the liver, the lateral peritoneal sheets do not meet above the alimentary canal to form a distinct mesentery. They are widely separated, and in the space between them the pericardial cavity is formed, just above the anterior lobe of the liver. The relations of the peritoneal and pericardial cavities are shown in diagram VI, which represents a cross-section through that region. For convenience of description, we may conceive of the pericardial sac as formed by an evagination of the peritoneal membrane on the right side into the space above the anterior lobe of the liver, and below the alimentary canal. The sac formed by this evagination is in turn *invaginated* by the pushing in of the heart (V) from below. In this way the pericardial membrane becomes arranged to form a double wall made up of two layers — an outer (O), or parietal layer, which encloses the pericardial cavity (pcc), and which is reflected to form the inner, or visceral layer (i), which immediately invests the heart. By the approximation of the pericardial layers, where they are reflected over the heart, a ventral cardiac ligament, the *mesocardium* (cm) is formed. The mesocardium partially separates the general pericardial cavity into two unequal divi-



sions, right and left. These two cavities communicate freely with each other dorsally (above and behind the heart), but are entirely separated ventrally. The right pericardial cavity, which is the larger, remains in free communication with the peritoneal cavity through the *pericardio-peritoneal foramen* (pcf). The heart has therefore exactly the same relation to the pericardium and the pericardial cavity as the intestine has to the peritoneum and the peritoneal cavity. There is only this difference, that the mesentery is *dorsal* to the intestine, while the mesocardium is *ventral* to the heart.

The right pericardial cavity may be described approximately as an elongated lenticular cavity, 2-3 cm. long, flattened dorso-ventrally, and lying just above the anterior portion of the anterior lobe of the liver. The anterior end of the cavity is larger and extends somewhat toward the right. It includes that portion of the cavity which contains the ventricle. The posterior end of the cavity is narrower, and extends backward and toward the left. The right pericardial cavity, as a whole, is bounded above by the dorsal body wall; below by the anterior lobe of the liver; internally by the mesocardium and the intestine (which it partially surrounds); and externally by the reflected peritoneum, which lies for the most part against the dorso-lateral body wall. An imperfect septum, the *portal septum*, complete only in the posterior region, is formed by the reflection of the roof into the right pericardial cavity. It extends parallel to the long axis of the cavity, and partially divides it into two chambers — a smaller *outer* and a larger *inner* chamber. This double-layered portal septum in the middle portion surrounds the portal heart; anteriorly, the anterior portal vein runs between its walls; and posteriorly it surrounds the common portal vein.

The *outer chamber* of the right pericardial cavity lies external to the portal septum. It is a narrow cavity, about 2-3 cm. in length, lying parallel to the inner chamber. It communicates with the inner chamber below the septum throughout almost its entire length. Only the extreme posterior portion of the outer chamber, into which the lateral wall of the alimentary canal projects, is completely separated by the septum from the inner chamber. In the posterior region the outer chamber communicates laterally and externally with

the general peritoneal cavity, through a narrow slit about 1-2 cm. in length — the pericardio-peritoneal foramen. (See Figs. VI, X, XIX, pcf). The direction of the slit is not quite longitudinal, but extends slightly outward anteriorly. The lower margin of the foramen is formed anteriorly by the fold extending upward from the liver (hepatic ligament) (See Fig. VI). Posteriorly, the slit borders on the lateral wall of the alimentary canal. The upper margin of the slit is formed posteriorly by the body wall and anteriorly by a reflection of the peritoneum from the wall. Through the pericardio-peritoneal foramen passes the supra-intestinal vein closely attached to the lateral wall of the intestine. The anterior extremity of the *right mesonephros* extends through the foramen, projecting from the inner side of the roof. The floor of the outer chamber is formed anteriorly by the upper surface of the anterior lobe of the liver; posteriorly, by the fold extending from the upper surface of the lobe to the lower margin of the pericardial foramen. The roof of the outer chamber is in direct contact with the body wall. External to the portal heart, toward the anterior end of the chamber, the *right pronephros* projects downward and outward into the cavity, pushing the pericardium before it. Just behind the pronephros, and above (outside) the pericardium, along the inner margin of the chamber, lies the anterior end of the mesonephros, which extends backward through the pericardial foramen, as described. In the posterior region the outer chamber lies against the right side of the intestinal wall. Along this wall a fold of the pericardium extends from the pericardial foramen to the posterior end of the portal heart. This fold encloses the *supra-intestinal* vein. (See Fig. XIII.)

The *inner chamber* of the right pericardial cavity lies internal to the portal septum, and encloses the ventricle of the heart. It is much larger than the outer chamber, being of about the same length, but wider and deeper. The inner chamber is situated slightly ventral to the outer. Anteriorly, the chamber is about  $\frac{3}{4}$  cm. deep. Posteriorly, it becomes shallower and narrower, terminating just anterior to the gall bladder, and above the anterior lobe of the liver. On the left side the inner chamber forms a blind sac into which a



lobe of the auricle projects. The roof of the inner chamber is in contact with the ventral surface of the alimentary canal. The floor lies upon the dorsal surface of the anterior lobe of the liver. The anterior wall lies against the connective tissue surrounding the last gill pouch on the right side. The external wall is formed by the portal septum, which is incomplete ventrally, leaving an extensive communication with the outer chamber. The inner wall is formed by the mesocardium, which is also incomplete. Above the mesocardium is a narrow longitudinal slit (about 1 cm. in length) through which the right and left pericardial cavities communicate. The ventricle of the heart occupies the anterior portion of the inner chamber. The double-layered mesocardium passes upward and outward from its attachment, soon dividing into two sheets which form the inner pericardial layer immediately surrounding the ventricle. (Fig. VI.) Anteriorly the inner pericardial layer becomes continuous with the outer, forming no pericardium. In this way the anterior end of the ventricle is *not covered* by the pericardium, but lies *outside* the pericardial space. The mesocardium is attached ventrally to the left margin of the anterior lobe of the liver. Posteriorly it encloses the sinus and veins opening into it.

The left pericardial cavity lies on the left side of the mesocardium, somewhat dorsal to the right cavity. It is a small elongated sac, which closely surrounds the auricle. The roof is in contact with the alimentary canal internally and the dorsal body wall externally. The floor and external walls touch the latero-ventral body wall. The inner wall is formed by the incomplete mesocardium, leaving the right and left pericardial cavities in communication dorsally. The exterior wall abuts against the postero-dorsal wall of the oesophagocutaneous duct. Posteriorly, the cavity ends as a short blind pocket. From the roof the left pronephros and the left anterior cardinal vein project into the cavity, pushing the pericardium before them. The mesocardium extends into the left pericardial cavity and surrounds the ventricle on the right side. The postero-internal angle of the auricle often extends through the slit-like foramen above the mesocardium, and lies in a pocket within the right pericardial cavity. This relation is not constant, however.

## ARTERIAL SYSTEM.

The *ventral aorta* (Figs. X, XVIII, Av.) consists of a principal median trunk, which divides anteriorly into a pair of lateral branches. The main trunk lies in the median line, just above the ventral body wall and below the pharynx. The length is about 3 cm. The lateral branches are a little longer. It extends from the anterior end of the ventricle to the posterior extremity of the "club-muscle." It lies between the last six or seven pairs of gills, and is imbedded in the peculiar brownish fatty connective tissue characteristic of that region. The median trunk of the aorta is nearly cylindrical in shape, but narrows slightly in caliber anteriorly. Posteriorly, at its junction with the ventricle, it is suddenly constricted. The relatively small opening from the ventricle is guarded by a pair of strong semi-lunar valves, as previously described. The short expanded portion of the aorta just beyond the constriction and behind the first gill branches represents the *bulbus aortæ*. This portion of the aorta is in contact ventrally with the dorsal surface of the anterior lobe of the liver.

The ventral aorta divides anteriorly into two branches (right and left) which pass forward, upward, and outward, along the dorso-lateral aspect of the posterior end of the club-muscle. The posterior end of the club-muscle, with reference to the point of branching, is variable, on account of the mobility of the former. The usual position is shown in Fig. X. But the muscle may be drawn forward, or even back below the point of division.

The *afferent branchial arteries* (Figs. X, XVIII, af. br.) rise on either side from the ventral aorta and its right and left branches. There are usually six or seven pairs arising from the median trunk, and from three to six pairs from the branches. Sometimes there is one more on one side than on the other, corresponding to the asymmetrical occurrence of the gills. The six or seven pairs from the median trunk are never symmetrically disposed. The last afferent branchial artery on the right side is always posterior to the corresponding left vessel. (See Fig. X.) The two pairs lying next anterior to the last are situated nearly opposite to each other,



while the remaining vessels from the median trunk are asymmetrical, the *left* vessels arising anterior to the corresponding vessels on the right side. The afferent branchial arteries arising from the right and left branches of the aorta are also asymmetrically placed, corresponding to the asymmetry of the gills. The afferent vessels vary in length, the anterior vessels being longer than those in the posterior region. Those from the main trunk are about 1-1.5 cm., while those from the lateral branches are 1.5-3 cm., increasing from behind forwards. The most anterior vessel is always the longest. In size they are all about equal. The direction of the arteries is external and slightly upward in the arteries from the main trunk, and forward, upward, and outward in those from the lateral branches. Each afferent branchial artery terminates on the postero-external wall of the corresponding gill pouch, just below the external gill passage.

The last afferent branchial artery of each side gives off a small branch a short distance from the gill. This branch possesses a lumen only at its origin, if at all. It soon becomes reduced to a slender string of connective tissue which becomes lost in the connective tissue around the "club-muscle." Attached to this string is a small spheroidal body, apparently made up of fibrous and fatty tissue. (See Fig. X, XIV.)

It may be remarked that in *Bdellostoma forsteri* this string may be traced from the branchial artery around to the dorsal aorta. The significance of these structures will be discussed later.

#### BRANCHIAL CIRCULATION.

(Figs. VIII, IX, X, XIII.)

The gills of the *Bdellostoma* are lens-shaped pouches, compressed laterally, so as to be concave on the inner face and convex on the outer. The pouches are not circular in outline, but more nearly elliptical, being elongated dorso-ventrally. The gill, as a whole, has two faces and four borders—superior, inferior, anterior, and posterior. The anterior and posterior are usually indented so as to be slightly concave, instead of convex. The afferent gill passage enters at the middle of the concave *inner* wall of the gill. (Fig. XIX.)

The efferent gill passage is given off from about the center of the convex *outer* wall. (Fig. X.) The line through these openings I shall call the axis of the gill. The internal anatomy is complex. The mucous membrane of the inner walls is folded to form a number of plates which are parallel to the axis of the gill and extended radially toward the center. (Fig. IX.) There are about twenty large plates, and a large number of smaller ones. The latter extend only a short distance in from the wall, and fill in the spaces between the bases of the other gill plates. Each plate is thrown into folds, only moderately near the base, but to an extraordinary degree of complexity toward the center. In this way a large amount of respiratory surface is developed. The free central margin, like the attached base of the plate, is strong and only slightly branched. These parts seem to serve merely as supports for the extremely thin respiratory leaflets. The inner surface of the gill wall, and the thicker supporting parts of the gill plates are covered with a stratified epithelium. The delicate respiratory leaflets are covered with a thin pavement epithelium. Next to the epithelial membrane occurs a small amount of connective tissue surrounding the blood vessels. Externally, the wall of the gill pouch is composed of a double layer of striated muscle—the external layer of *circular* fibers, the internal of *longitudinal* fibers (parallel to the axis). Surrounding the muscular layer is a thin serous membrane, which lines the lymphatic peri-branchial spaces.

The general distribution of the blood vessels in the gills is as follows: The *afferent branchial artery* of each gill passes under the lower margin of each gill pouch, then upward over the convex outer gill wall, which it enters just below the external gill passage. Some small twigs are given off which supply the gill passage and the muscles of the gill wall. The afferent artery then divides into two branches which surround the opening of the gill-passage, forming an irregular "ring vessel." From this "ring vessel" several radial vessels, often dilated into sinuses, are given off which pass within the gill wall toward the peripheral margin. Branches are given off which extend along the attached margin of each gill plate, beneath the muscular layers of the gill wall. From these branches numerous smaller vessels pass directly into



the gill plate. Their general direction is parallel to the axis of the gill, and perpendicular to the walls of the gill pouch. These smaller vessels break up into capillaries, which ramify between the thin epithelial walls of the respiratory gill leaflets. In this region an extensive capillary network is formed, and anastomoses between the larger vessels are also common. Toward the opposite (*i. e.* the inner) attached edge of the gill plate, and in the free central margins, the capillaries again unite to form larger vessels. These efferent branchial vessels converge on the inner wall of the gill pouch in much the same way as they are distributed in the outer wall. They unite under the muscular layer into sinuses and vessels which finally unite to form the efferent branchial artery of each gill pouch. This vessel leaves the gill wall just above the internal gill passage. (Fig. XIX, ef, br.) A diagrammatic representation of the branchial circulation is shown in Figure XIII, which represents the vascular distribution in a plane parallel to the gill axis. Figure IX shows a drawing of a section of an injected gill made perpendicular to the axis of the gill, and near its center. The low magnification fails to give an adequate idea of the great complexity in the formation of the gill leaflets. Figures VIII and XIV represent small portions of these leaflets magnified to show the capillary vessels, which are composed of a single layer of epithelial cells. The larger vessels have walls composed of three layers,—an outer layer of connective tissue, a middle layer of circular muscle fibers, and an inner simple endothelial layer.

The *efferent branchial arteries* (Figs. XVIII, XIX, XX, ef, br) arise from the inner face of each gill pouch, just above the internal gill passage (gpi). Each efferent vessel extends upward and inward toward the median line. In the posterior region each vessel ascends just behind a "gill constrictor" muscle, then turns forward immediately *above* it and joins the overlying common carotid just anterior to the muscle. There are never *two* efferent vessels for each gill-pouch, as is commonly the case in *Bdellostoma forsteri*. All the efferent branches of each side open into the corresponding lateral common carotid.

## GENERAL ARTERIAL SYSTEM.

The *common carotid arteries* (right and left) posteriorly extend longitudinally along each side above the gills and beside the pharynx. (Figs. XVIII, XIX, XX, Car.) Externally, they connect with the efferent branchial arteries; and internally, by means of from four to seven short commissural vessels (comv) on each side, they communicate with the median dorsal aorta. These commissural vessels usually arise nearly opposite the fourth or fifth to the eighth or tenth pairs of gills. Posteriorly the common carotids are connected with the dorsal aorta nearly opposite each other, and a short distance behind the last pair of gills. Anteriorly they continue forward on each side of the pharynx, giving off numerous small twigs to this organ. Each carotid also supplies the club muscle with several branches. The most posterior pair of these branches seem to supply only that portion of the muscle connected with the longitudinal *retractor* fibers. The remaining branches supply the circular *constrictor* portion. The branches to the "club-muscle" run in the sheet of connective tissue which connects the muscle to the dorso-lateral body wall on each side.

Just behind the cartilaginous "pharyngeal basket" of the branchial skeleton, each common carotid divides into two branches, the *external* and *internal* carotid arteries. Each external carotid passes forward and downward around and outside the pharyngeal basket and runs forward along the outer margin of the basal plate. Near the junction of the posterior with the anterior segments of the basal plate, a small branch is given off which passes upward and inward to the ligament attaching the dental plate (*ramus lingualis*). This branch supplies the dental plate but apparently not the muscles moving it. The main trunk of the external carotid then passes forward along the external margin of the basal plate on each side giving off small twigs to the lateral walls of the skull. Anteriorly it breaks up into a number of small branches, which supply the muscles and integument in the tentacular region.

Each *internal carotid* continues inward and forward just above the pharynx. (See Figs. XVIII and XX.) A rela-



tively large lateral branch is given off on each side which runs forward and supplies the muscles in the lateral region of the head. In one instance I traced this vessel (on the left side), forward under the lateral trunk muscles just outside the skull wall, under the hyoid arch, and out into the orbital region, sending a branch out to the skin, in the fibrous band of connective tissue just below the eye. The main trunk of the internal carotid joins the corresponding vessel of the opposite side in the median line just below the notochord and in front of the supra-pharyngeal plate. (See Fig. XX.)

The *vertebralis impar* (v), formed by the junction of the internal carotids, runs forward a short distance in the median line beneath the notochord, giving off branches to the brain and cranial wall. Passing below the cranium, just behind the pituitary sac, it divides into two lateral branches, right and left, which run forward on each side of the base of the cranium to the nasal and anterior head region.

The *anterior dorsal aorta* (Figs. XVIII, XIX, XX, Aa) is that portion of the median dorsal aorta which lies in, and in front of, the gill region. Posteriorly, it begins with the most posterior point of connection with the lateral carotids. It lies immediately above the pharynx, and below the notochord. In the gill region, the anterior dorsal aorta gives off four or five pairs of branches to the body wall (somatic branches). The posterior, three pairs of these usually pierce the overlying "gill constrictor" muscles. In the anterior gill region, the aorta curves slightly to the right, and continues forward beneath the right side of the notochord. In one instance it turned first to the left, ran forward two or three somites, then passed over to the right and forward as usual.

Anterior to the gill region it gives off in its course seven or eight pairs of somatic branches to the adjacent segments of the body wall. In general, an artery is given off to each alternate myoseptum on each side. Each somatic vessel divides into two branches, dorsal and ventral, whose course is the same as that of those to be described in the abdominal region (see Fig. XV). There are some variations in the distribution of the branches of the anterior dorsal aorta,

however. The arteries, like the corresponding myotomes, are not arranged in bilateral symmetry. The branches are given off *alternately*, especially in the anterior region. (See Fig. XX.) A short distance behind the junction of the internal carotids, the anterior dorsal aorta crosses over and joins the left internal carotid, just behind the origin of the lateral branch.

The *posterior dorsal aorta* (Figs. XII, XV, XVIII, XIX, XX, Ao), is the posterior continuation of the same vessel which anteriorly forms the anterior dorsal aorta. Beginning behind the junction with the lateral carotids, the posterior dorsal aorta gives off branches as follows:

(a) A pair of *somatic branches*, and usually a mesenteric twig to the intestinal wall.

(b) Twigs to the right and left *pronephros* (pnl, par). These may come off as separate twigs, but usually arise in common with somatic branches (Fig. XIX).

(c) The *coeliac artery* is a relatively large vessel. It occasionally gives off a twig to the left pronephros. It then passes downward between the sinus venosus and the alimentary canal (to which it gives off a small branch). The coeliac artery then proceeds along the common bile duct to the gallcyst, which it supplies. Then it divides into two terminal vessels, anterior and posterior, which pass along the bile ducts to the anterior and posterior lobes of the liver. Here they break up into capillaries which supply these structures.

(d) *Mesenteric arteries* (Figs. XII, XV, XVIII, mes) are given off ventrally, which pass downward between the right and left posterior cardinal veins, in the mesentery, to the intestinal wall. Just above the intestinal wall they usually divide, one branch going to the right, the other to the left side of the intestine. Both branches pass to the left of the supra-intestinal vein, but pass one on each side of the vagus nerve, which lies in the median line just above the intestinal wall. There are about thirty mesenteric arteries, and they arise in a somewhat irregular manner. Often, however, they arise in couples, one a short distance behind the other (See Fig. XII).

(e) The *somatic arteries* arise regularly along the entire length of the dorsal aorta, anterior and posterior (Figs. XII,



XV, XVIII, XX, s). The somatic arteries, as a rule, alternate with the somatic *veins* on each side. (Fig. XII.) Those of the right and left sides are sometimes in pairs, opposite each other, but usually alternate, always corresponding to the arrangement of the myotomes on each side. The somatic arteries from the *anterior* dorsal aorta arise independently. Those from the *posterior* dorsal aorta usually arise by a short trunk in common with one or more renal branches (Fig. XII). Each somatic artery passes above the mesonephros, supplies it with one or more twigs, and then divides into two branches. (See Fig. XV.) The *dorsal* branch passes directly upward beside the notochord, supplying the lateral trunk muscles, and sending branches into the neural canal to supply the spinal cord. Then it passes up in the median longitudinal septum above the neural canal. It passes out to the skin of the dorsal region through the sheet of connective tissue which fastens the skin to the body wall.

The *ventral* branches of the somatic arteries correspond to the *intercostal vessels* of the higher vertebrates. (Figs. XII, XV, ic.) They pass outward along the roof and sides of the peritoneal cavity, between the lateral trunk muscles and the peritoneum. They pass along the septa between the myotomes, giving off many minute twigs to the adjoining muscles. (See Figs. XII, XV, ic.) Each "intercostal" passes along with (anterior to) the corresponding intercostal nerve (sn). After passing between two slime glands, which it supplies, each intercostal vessel gives off irregular branches to the ventral rectus trunk muscle in the vicinity. The end piece of each vessel passes out into the skin in the neighborhood of the slime glands, and is distributed to the integument of the ventral and lateral regions of the body.

(f) *Renal branches* are supplied segmentally to the mesonephros along each side of the aorta. A portion of these are shown in Figure XII, (r). (cfr. also Figs. XVIII and XX.) These renal branches supply the segmental glomeruli along the inner wall of the mesonephros. The glomeruli correspond to the myotomes only in a general way, and not exactly. Usually two glomerular vessels, and one or more twigs to the dorsal and inner walls of the mesonephros, arise from a common trunk with a somatic branch. There is

much variation in this respect, however. Sometimes a somatic and one renal vessel arise together, and sometimes the renal vessels arise independently.

(g) The *genital branches* (Figs. VII, XVIII, XX, gen) arise from all the mesenteric arteries in the region of the testis in the male, and the ovary in the female. Occasionally branches arise independently from the dorsal aorta. The genital branches pass out in the genital ligament (a special fold on the right side of the mesentery). Soon after entering this fold the genital vessels, for the most part, unite to form a longitudinal commissural vessel. (Fig. VII.) From this vessel a large number of smaller vessels run out toward the testis or ovary, branching and anastomosing freely. A capillary network is formed in the membrane surrounding each ovum, or lobule of the testis.

Behind the cloaca, the aorta continues immediately below the notochord in the median line, but here, as might be expected, only the somatic branches are given off. On reaching the median ventral plate, the aorta divides into a right and a left branch, each of which passes backward on the corresponding side of the plate. Lateral branches are given off to supply the muscles and integument of the caudal region. In the caudal fin, small vessels run out distally corresponding to each fin ray.

#### GENERAL VENOUS SYSTEM.

The *veins* of the Bdellostoma may be included under two separate systems—the *general* system, and the *portal* system. The general venous system is larger, including all those veins through which the blood flows into the sinus venosus. (Figs. X, XI, XVII, XVIII, S.) Anteriorly where it empties into the auricle, the sinus is narrow, and receives the *inferior jugular vein* (jv). Posteriorly, behind the auricle, the sinus is dilated, and receives on the left, the *left anterior cardinal vein* (acl.) anteriorly, and the common cardinal vein (pcc) posteriorly. On the right side enter the anterior and posterior *hepatic veins* (ha, hp).

Beginning with the general venous system in the head region, we find the *superficial anterior cardinal vein*. (Figs.



XVII, XVIII, scd) arising on each side of the head. It leaves the cranium just dorsal to the corresponding vagus nerve. It passes backward alongside the vagus, between the lateral trunk muscles, and the constrictors of the pharynx. In this region it receives the first eight or ten somatic veins. These somatic veins, like the somatic arteries (with which they alternate), arise from the skin and trunk muscles the entire length of the body. They correspond exactly to the somatic veins of the abdominal region shown in Figure XV, (s). They are each composed of a very short terminal trunk which is supplied by two branches, (1) a *dorsal* branch which collects the blood from the dorsal region of the integument, the spinal cord, notochord and muscles of the vicinity. It descends vertically at the side of the notochord, and on reaching the ventral surface of the dorsal body wall, joins with (2) the *ventral* branch, or "*intercostal*" vein. The intercostal veins, like the intercostal arteries, are distributed to the integument of the ventral and lateral regions of the body, and the ventral rectus muscle. In the gill region, the intercostals receive, in the region of the slime glands, occasional "*pleural*" branches from the connective tissue. Then after collecting the blood from the two adjacent slime glands, it passes between these along the intermuscular septum of the myotomes, on the ventral surface of the dorsal and dorso-lateral body walls. The intercostal veins lie just in front of the corresponding intercostal nerves. As before mentioned, the intercostal veins usually alternate with the intercostal arteries (Figs. XI, XII, XV, XIX, ic), especially in the abdominal region. In the pharyngeal region the arrangement is less regular, there being often two adjacent arteries or veins, and occasionally both an artery or vein on *one* intermuscular septum. (Fig. XIX.) After receiving the somatic veins from the head region, the superficial cardinal pierces the constrictor muscle and joins the *deep cardinal* vein.

The *deep anterior cardinal* vein (Figs. XVII, XVIII, dcd) arises from the integument and muscles of the anterior head region. It passes on each side between the pharynx and hyoid arch (just below the posterior process), then directly backward alongside the pharynx, internal to the constrictors,

receiving branches, and passing under the first branchial arch, but over the second. About 2-3 cm. behind the second arch it is joined by the *superficial cardinal* to form the *common anterior cardinal vein*.

The *common anterior cardinal* (or jugular) veins, right and left (Figs. XVII, XIX, acr, acl), pass backward and beside the pharynx, just external to the corresponding carotid artery, and internal to the vagus nerve. They receive four sets of branches: (1) somatic veins from the body wall; (2) pharyngeal branches, (ph), numerous small twigs from the wall of the pharynx; (3) "club-muscle" branches, from the "club-muscle;" (4) "pleural" branches from the connective tissue in the pharyngeal region. Anteriorly, the courses of the right and left anterior common cardinals are similar. Behind the "club-muscle," however, they are quite different.

The *left anterior cardinal* continues in the same general direction backward beside the vagus, and above the gills. It receives the usual somatic branches, and also a few "pleural" twigs from the connective tissue surrounding the gill pouches. It also occasionally receives twigs from the walls of the gill passages and oesophago-cutaneous duct. Posteriorly (Fig. XI, acl), it forms a slight projection from the roof into the left pericardial cavity, as before described. It passes between the left pronephros, from which it receives a twig, and the alimentary canal, and empties into the antero-lateral angle of the dilated posterior portion of the sinus venosus.

The *right anterior cardinal*, on the other hand, toward the posterior end of the "club-muscle," leaves the pharyngeal wall, passes downward toward the posterior end of the "club-muscle," and crossing over toward the median line, empties into the *inferior jugular vein*. (Fig. XIX, jr) The remaining area corresponding to that supplied by the left anterior cardinal on the other side of the body is supplied by the portal system.

The *inferior jugular vein* (Figs. X, XVII, XVIII, jr) arises from the posterior end of the "club-muscle," from which it emerges on the ventral surface. It passes backward a little to the left of the median line, immediately over the ventral body wall. After receiving the right anterior cardinal



vein, it continues backward a little below and to the left of the median ventral aorta. (Fig. X.) It receives a varying number of branches from the body wall. It also receives several small "pleural" twigs from the connective tissue and gill passages, including the oesophago-cutaneous duct and the adjoining pharyngeal wall. Finally, the inferior jugular vein empties into the anterior end of the sinus venosus, just in front of the sinu-auricular aperture.

The *posterior cardinal veins* arise in the caudal region from small twigs which form two small veins. These lateral veins accompany the arteries on each side of the cartilaginous median ventral plate in the caudal region. (Fig. XVII.) They unite to form the *median caudal vein* (caud), which runs forward immediately beneath the caudal artery. The caudal vein, at its posterior end, is dilated to form a small sinus just in front of the median ventral plate. Laterally, the caudal vein receives, on each side, the somatic veins of the caudal region.

Anteriorly, in the cloacal region, the caudal vein divides into two veins, the *right* and *left posterior cardinal veins*. (Figs. XI, XII, XV, XVIII, XIX, pcr, pcl.) These vessels run parallel with each other, just below and on each side of the posterior dorsal aorta. The right posterior cardinal is much smaller than the left. (See Figs. XII, XV, XVII.) Each lies internal to and in contact with that side of the corresponding mesonephros which faces toward the median line. The posterior cardinals are joined by a large number of short transverse commissural vessels (about twenty-five in all). They are not placed at regular intervals, but are more numerous in the posterior region. They vary in size, being usually about as wide as the *right* cardinal vein. The posterior cardinals receive two sets of branches: (1) the renal branches; (2) the somatic veins.

The *renal branches* (see Fig. XII), appear to arise, for the most part, on the ventral surface of the mesonephros. They collect together and form small twigs, which run across toward the median line and empty into the corresponding posterior cardinal vein. These renal veins are somewhat irregularly distributed, but traces of their original segmental arrangement are easily recognized.

The *somatic* veins have already been described in a general way. Those of the abdominal region pass dorsal to the corresponding mesonephros (receiving no branches from them), and empty into the corresponding posterior cardinal vein.

The posterior cardinals receive no veins from the intestine. In one instance only I observed a branch from the testis running upward into the right posterior cardinal vein.

Anteriorly, a short distance behind the heart, the right and left posterior cardinals unite again to form the unpaired *posterior common cardinal vein* (Fig. XVII, pcc), which passes forward on the left side, and empties into the posterior end of the sinus venosus.

The *sub-intestinal vein* (Figs. XI, XV, XVII, XVIII, sub. int.) arises from the ventral wall of the intestine toward the anterior end. It passes forward along the median ventral line of the intestinal wall, and on reaching the hepatic ligament, passes down along its posterior margin to the posterior lobe of the liver. (Fig. XI.) In some specimens it passes through the tissue of the liver for a considerable distance, but in others it runs along the surface, within the serous membrane. It passes behind the liver, and runs forward on its ventral and external aspect. It receives branches from the posterior lobe of the liver, and becomes the posterior hepatic vein (hp). As such it passes upward, parallel and near to the bile duct of the posterior lobe. It becomes very much widened, and finally empties into the posterior end of the sinus venosus, opposite the common posterior cardinal vein.

The veins of the anterior lobe of the liver converge to form the *anterior hepatic vein*, which lies on the dorsal surface of the lobe. (Figs. XI, XVII, XVIII, ha.) This vein runs forward and upward, emptying into the left side of the sinus venosus, a little behind the sinu-auricular opening.

There is also apparently a small vein running in the ligament between the anterior end of the posterior lobe, and the posterior end of the anterior lobe. The veins from the gall cyst, as will be seen, join the portal system, and will be described there.



## THE PORTAL VENOUS SYSTEM.

The portal venous system includes the portal vein and all the vessels which flow into it.

The *anterior portal vein* (Figs. XVII, XVIII, XIX, ap) arises in the right branchial region, a little in front of the posterior end of the "club-muscle." (Fig. XIX.) It lies just below and to the right of the notochord, and receives the somatic veins from the right side in the branchial region. A few scattering venous twigs from this region also pass across into the inferior jugular vein. The anterior portal continues backward into the fold (portal septum), separating the inner and outer chambers of the right pericardial cavity, as previously described. It passes between the alimentary canal and the right pronephros, and opens into the roof of the portal heart near the anterior end. The entrance is guarded by a pair of thin membranous valves, semi-lunar in shape, one anterior and one posterior. (See Fig. XVI, ap.) Just before entering the portal heart it receives a branch which is made up of a twig from the pronephros, and (often) two or three somatic veins lying opposite and posterior to the portal heart. In one instance, I observed an anastomosis between this vein and a somatic vein emptying into the right posterior cardinal vein.

The *supra-intestinal vein* (Figs. XI, XII, XV, XVII, XVIII, XIX, supr. int.) receives the blood from the entire intestinal wall, excepting the floor in the anterior region. It runs forward just above the intestine a little to the right of the median line, within the mesentery. It lies to the right of the vagus nerve and the mesenteric arteries. In the region of the reproductive organs the supra-intestinal vein receives several *genital veins* which descend in the mesentery. These veins are formed by the plexus of small venous twigs in the special genital fold of the mesentery (Figs. XII, XVIII, gen). On reaching the pericardial region, the supra-intestinal vein turns to the right side of the intestine. Here it receives the *cystic vein* (Fig. XIX, cv), which is made up of branches from the gall cyst. The supra-intestinal vein then passes through the pericardio-peritoneal foramen, beside the intestine, and below the right mesonephros. It then crosses

the roof of the outer chamber of the right pericardial cavity just below the right vagus nerve, and enters the roof of the portal heart near the posterior end. (See Fig. XVI, *supr int.*) The slit through which the blood enters is diagonally placed, and guarded by a pair of semi-lunar valves, like those of the anterior portal.

The *portal heart* (Figs. X, XVI, XVII, XVIII, XIX, H.) lies in the pericardial fold which forms the septum in the right pericardial cavity. It is an elongated sac (1-2 cm. in length), somewhat irregular in shape and variable in size. It stretches diagonally across the pericardial cavity, and lies nearly opposite the ventricle (cf. Fig. X). Anteriorly it receives the anterior portal vein; toward the posterior end it receives the supra-intestinal vein. Both these enter dorsally. At its posterior extremity the portal heart empties into its efferent vessel, the *common portal vein*. The opening into the common portal vein is guarded by a pair of strong semi-lunar valves (Fig. XVI, cp), which are placed laterally, and like the other valves previously described, prevent any reflux of blood during the circulation.

Johannes Müller was mistaken in his statement that no muscle fibers exist in the portal heart of *Bdellostoma*.<sup>\*</sup> The wall is quite muscular, fully as much as that of the auricle. As in the latter, the inner surface of the wall of the portal heart is made irregular by muscular and fibrous trabeculæ, which project from the surface. The muscle fibers are *distinctly striated*, and their nuclei seem to lie on the sides of (not within) the contractile fibers.

The *common portal vein* (Figs. XVII, XVIII, XIX, cp) continues backward and inward toward the median line. It passes above the anterior lobe of the liver, to which it gives off ventrally a large branch which descends almost vertically alongside the hepatic duct of the anterior lobe. (XI, cpa). The main trunk of the common portal vein then crosses the median line to the left side and passes backward and downward alongside the hepatic duct of the posterior lobe. (Fig. XI, cpp.) About the center of the dorsal surface it enters

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<sup>\*</sup>Vergl. Anat. der Myxinoiden (1834). Later Müller observed the pulsations of the portal heart in living Myxine. Untersuchungen über die Eingeweide der Fische (1842).

the posterior lobe and breaks up into capillaries in the tissue of the liver.

I have observed in several cases a marked tendency for the injected carmine gelatine to escape from the blood vessels into the surrounding lymphatics, which are very numerous and extensive. These lymphatic spaces, especially the subdermal spaces in the caudal region, and the peri-branchial spaces around the gill pouches, are usually found more or less injected, although the blood vessels show no signs of overdistension. The lymphatic spaces around the vessels in the gill itself are also often filled. This condition may be interpreted as indicating that the capillary walls are unusually weak and permeable, so that the injected liquid passes through them, carrying blood corpuscles with it. That this process is not normal is shown by the absence of red blood corpuscles from these lymphatic spaces in life, and in uninjected specimens.

#### REMARKS ON COMPARATIVE ANATOMY OF BDELLOSTOMA.

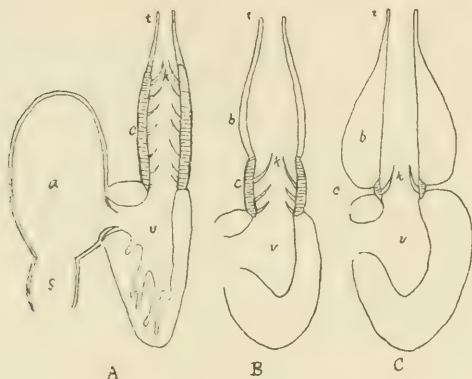
The communication of the pericardial cavity with the peritoneal cavity through the pericardo-peritoneal foramen is primitive. The heart, which is a specialized portion of the primitive sub-intestinal vessel, always develops at first in the anterior end of the general peritoneal cavity. In all adults, however, a special pericardial cavity is formed. In *Petromyzon*, whose pericardial sac is enclosed in a cartilaginous pocket, the separation is complete. In the larval *Ammocœtes*, however, there exist two larval pericardio-peritoneal foramina, one on either side. Communication between pericardial and peritoneal cavities exists also in *Elasmobranchs* and *Ganoids*, but only during embryonic life in all higher vertebrates.

Although its embryological development is not yet worked out, the sinus venosus doubtless at first receives a right and left *ductus Cuvieri*, like *Petromyzon* (Goette), and higher forms. The right ductus has probably been lost altogether in a manner which will be discussed later. The left ductus *Cuvieri* has apparently fused with the sinus venosus, and is represented by the external portion of the posterior expanded



division of the sinus, which still receives the right anterior and posterior cardinals.

In the absence of a contractile valved *conus arteriosus*, Bdellostoma and all the Cyclostomata resemble the Teleosts more than the Elasmobranchs. (See text figures A, B, C.)



A, Elasmobranch.

B, Ganoid.

C, Teleost.

s, sinus venosus.

a, auricle.

v, ventricle.

c, conus arteriosus.

b, bulbus arteriosus.

t, ventral aorta.

k, valves.

(From Boas's Zoology.)

In this respect the Bdellostoma is probably not primitive, since in the Sharks and Ganoids there is clearly a tendency to a reduction in the number of the valves and the size of the conus.\*

Contrary to Müller's statement (Vergl. Anat. der Myxinoïden, pp. 180), the bulbus aortæ is *not* entirely devoid of muscular fibers. As in the arteries in general, there is a small amount of plain muscle fibers mixed with the thick layer of elastic fibers. The bulbus is evidently not contractile, however, in the ordinary sense of the word.

\*It is quite possible, however, that the absence of a conus represents a condition more primitive than the Elasmobranch. No valved conus appears during the development of Petromyzon.

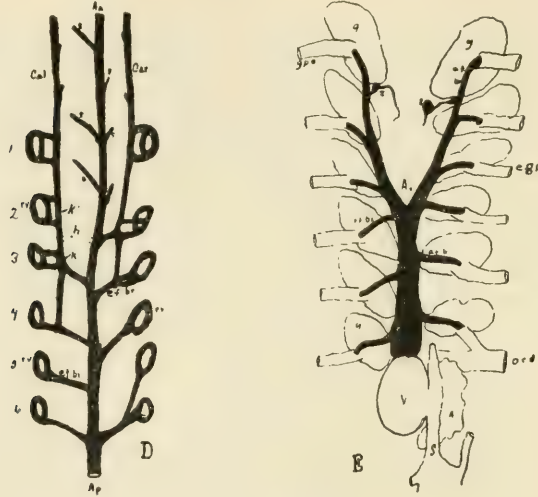
Variations from the structure of the typical ventral aorta, as previously described, are very common. As an extreme instance, I may mention a case mentioned by Müller, in which the ventral aorta, immediately after leaving the heart, divided into two branches from which all the afferent branchial arteries arise.

With respect to the "ductus Botalli," Müller noted the following in *Bdellostoma forsteri*:" "Ehe wir die Gefässe der Myxinoiden ganz verlassen, müssen wir noch einer Beobachtung gedenken, welche auf einen Entwicklungszustand des Gefäss-systems der Myxinoiden einiges Licht wirft. Ich habe nämlich bei dem grossen Myxinoid vom Cap wiederholt die Reste zweier ductus Botalli bemerkt, welche früher ohne Zweifel die *arteria branchialis* mit dem Arterien system in Verbindung setzten, jetzt aber ganz feine fadenartige Stränge bilden, deren Ursprung aus der *arteria branchialis* und Ende in Arteriensystem des Körpers aber noch hohl sind. Dieser Faden entspringt aus dem Aste der Kiemenarterie zur vordersten Kieme, in gleicher Weise auf jeder Seite. Bei seinen Ursprung ist er ansehnlich dick, conisch und hohl, die Fortsetzung ist aber sehr fein sie geht vorwärts aufwärts gegen die Carotis hin, wo diese aus den vordern Kiemenvenen entsteht, hier erweitert sich der Faden wieder, wird wieder hohl und senkt sich in die Anfang der Carotis ein. Aus diesem hohlen Ende des Fadens gehen einige feine Zweige zu den Pleuren ab. Diese Anordnung fand ich in gleicher Weise bei mehreren grossen Exemplaren von *Bdellostoma forsteri*. Ich habe sie auch bei den *Myxinen* gesehen. Diese obliterirten ductus Botalli waren offenbar früher weite Aortenbogen von dem *truncus arteriosus* des Herzens zu den Carotiden und von diesen weiter zur Aorta." (loc. cit., pp. 191.)

I have already described the same structures found in *Bdellostoma dombeyi*. In addition to the observation of Müller, I have added that a spheroidal or flattened mass of connective tissue is found attached to the "ductus" a short distance from its origin. This body is larger and more saccular in appearance in *Bdellostoma forsteri*. (See text figure E, z), and evidently may be interpreted as the rudiment of the *gill pouch* corresponding to the obliterated branchial artery. A similar ductus Botalli from the first branchial

artery is found in certain Caducibranchiata. In these cases, a "rete mirabile" persists in the course of the ductus, and represents the obliterated gill. (Balfour, Comp. Embryol. Vol II.)

Since the "ductus Botalli" is a constant feature in all specimens of *Bdellostoma* examined, its significance lies in



D, efferent branchial system of *Bdellostoma forsteri*, dorsal view.

E, heart and afferent branchial system of *Bdellostoma forsteri*, ventral view.

Ap. posterior dorsal aorta.

Aa, anterior dorsal aorta.

Car, right carotid.

Cal, left carotid.

ef. br, efferent branchial artery.

rv, ring vessel of gill passage.

S, sinus venosus.

A, auricle.

V, ventricle.

Av, ventral aorta.

afb, afferent branchial artery.

z, body on "ductus Botalli."

g, gill pouch.

gpe, external gill passage,

ocd, oesophago-cutaneous duct.

the fact that even in the 13-gilled forms, we have to do with a *reduction* rather than an *increase* in the *primitive number of gills*. The embryological development, according to Price (Some Points in the Development of a Myxinoid. Verh. der Anat. Ges., 1896), renders this conclusion certain. A large



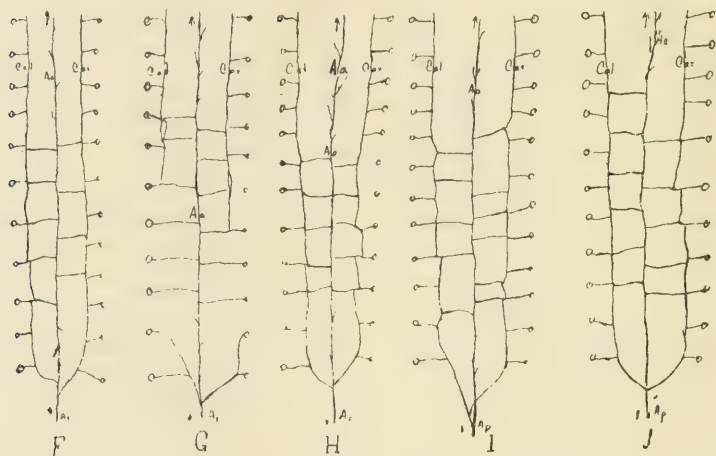
number of gill pouches (possibly thirty-five pairs) arise during the course of development. Of these, only the posterior 10-14 pairs remain to form the permanent gills of the adult.

The distribution of branchial vessels, one to each gill cleft (gill pouch), is a character in which the Myxinoids differ from all other Vertebrates. Even in *Petromyzon*, each afferent and efferent vessel is distributed to the *hemibranch* of *two different pouches*, the gill arteries corresponding to *gill-arches* rather than *gill clefts*. It is probable that the Myx-enoid condition is not primitive, although the embryological development is not known. A probable explanation of the manner in which this unique condition has been derived from the primitive arrangement is suggested by an examination of the efferent branchial vessels and their connections in *Bdellostoma forsteri* (see text figure D.) Here we find, usually, *two efferent branchial vessels* (ef, br) arising from the ring vessel (rv) which surrounds the gill passage on the wall of the gill pouch. These efferent vessels unite with the lateral carotid vessels, and with the dorsal aorta by anastomoses. This is an interesting intermediate stage between the arrangement of the vessels in *Bdellostoma dombeyi* (see Plate III, Fig. XX), and the ordinary vertebrate type. Referring again to text figure D, suppose, for example, we take afferent vessels from gill 3. If we fuse the two vessels together (which is almost accomplished in the sixth gill, right side), or obliterate one of them, we get *one* efferent vessel for each gill, as in gills 4, 5, and 6, left side. This is the condition in *all* the gills of *Bdellostoma dombeyi*. But if we break the connection at k, gill 3, and k<sup>1</sup>, gill 2, and at the same time connect the artery between them with the dorsal aorta by a vessel, h (dotted outline), this vessel, h, would be an *efferent branchial artery* of the *usual vertebrate type*. It would receive the blood from the posterior hemi-branch of gill 2, and the anterior hemi-branch of gill 3. I have no doubt that this very relation would be found as a variation, if a large number of specimens of *Bdellostoma forsteri* were examined.

A consideration of the extreme variability of the blood vessels in *Bdellostoma* renders this explanation all the more probable. To give a more adequate idea of the nature and extent of variation, I have made diagrams to show the rela-

tion between the efferent branchials, carotids, and dorsal aorta, as I found it, in five specimens of *Bdellostoma dombeyi*, taken entirely at random.

The variations apparently have no constant relation to the size or sex of the specimen. The number of efferent vessels, of course, varies with the number of gills.



F, G, H, I, J. Diagrams of the efferent branchial arteries and their connections (dorsal view) in *Bdellostoma dombeyi*. Lettering same as in plate figures (q. v.)

As a result of his studies of the blood vessels of *Chlamydo-selachus*, Dr. Ayers (*Morphology of the Carotids*, Bul. Museum. Comp. Zool., Harvard. Vol. XVII, No. 5, p. 211), reaches the following conclusion: "It is likewise obvious that the carotid vessels cannot strictly be said to arise from, or constitute the remains of, any particular pair of aortic arches, but represents all that is left of the commissural trunk from the most anterior arch of the ancestral form to the most anterior arch of any existing form." *Bdellostoma* and the *Myxinoid* type would seem to indicate rather the origin of the carotid arteries from a longitudinal trunk connecting *all* the efferent branchial vessels on each side.

I have not as yet been able to work out fully the distribution and homologies of the blood vessels in the head region. This problem, on account of its difficulty and importance, is reserved for a special paper. I may mention, however, that

the extension forward of the sub-chordal dorsal aorta into the head region as the *vertebralis impar* (*vertebralis impar capitis*, of Müller; *cranial aorta*, of Ayers) is probably a primitive character. This vessel occurs in *Chlamydoselachus*, as well as the *Cyclostomata*.

Müller describes a vein in *Bdellostoma forsteri* which runs from the right pronephros to the posterior cardinal. Only once have I found a similar vessel in *Bdellostoma dombeyi*. The vein which he describes from the intestine to the common posterior cardinal is also apparently lacking in *Bdellostoma dombeyi*.

In *Petromyzon*, as in most Vertebrates, but unlike *Bdellostoma*, the genital veins open into the posterior cardinals instead of the supra-intestinal vein. The difference in size between the right and left posterior cardinals is only one example of the great asymmetry of the venous system which is so characteristic of *Bdellostoma*.

The sub-intestinal vein\* is the homologue of the large ventral vein in *Amphioxus*, and the embryonic sub-intestinal vein of higher vertebrates. Judging from the development of *Petromyzon* (Goette, *Entwicklungsgeschichte des Flussneunauges*) and other forms, the sub-intestinal vein at first probably supplied the entire intestine, and was continued posteriorly into the caudal vein. The connection of the caudal vein with the posterior cardinals is very probably here, as elsewhere, a secondary arrangement. The reduction in the size and extent of the sub-intestinal vein is correlated with the development of the supra-intestinal vein. It is interesting to note that in *Bdellostoma* the sub-intestinal vein *does not break up into capillaries in the liver* to form a portal system, although it runs over the surface of, and even *through* the liver tissue. This is evidently an extremely primitive character, for the same relation is found in the early *embryonic* development of the same vessel in *Petromyzon* (Goette, loc. cit.), and all higher Vertebrates. According to Willey ("Amphioxus and the Ancestry of the Vertebrates") it is yet doubtful whether the sub-intestinal vein in *Amphioxus* forms a *true* capillary portal system, or merely passes through

\*It is a remarkable fact that the presence of this vein in *Bdellostoma* has apparently been overlooked heretofore by all observers, including Johannes Müller.



a system of small sinuses *outside the liver proper*. In all Vertebrates above *Bdellostoma* (including *Petromyzon*), the sub-intestinal vein in the adult forms a part of the portal system.

The inferior jugular vein when median and *unpaired*, as in *Petromyzon* and some of the higher fishes, always empties into the sinus venosus. When *paired*, as in other fishes, it empties into the ductus Cuvieri on each side. Müller recognized that the posterior end of the right anterior cardinal represented the inferior jugular of other forms, but did not describe it as such. According to him (Vergl. Anat. der Myxinoiden, p. 209), the inferior jugular always originates in the hyoid arch and the under side of the operculums. It also commonly receives branches from the muscles of the pharynx, *venæ branchiales inferiores* and *venæ nutritiæ* of the gill arches. Its origin in Myxinoids is dorsal to the ventral aorta, but its course is ventral to it. The large "club-muscle," therefore, has a *double* venous supply. The "retractor" portion is supplied by the inferior jugular vein; the "compressor" portion by the lateral anterior cardinals (jugulars).

The anterior cardinals (or jugulars) of *Bdellostoma* agree in all essential respects with those in other fishes, excepting the posterior end of the right cardinal. From the probable ancestral form, as represented in Elasmobranchs (viz., symmetrical cardinals, anterior and posterior, flowing into right and left ductus Cuvieri on each side) the present arrangement in *Bdellostoma* may easily have arose as follows: 1. An anastomosis was formed between the right anterior cardinal and the inferior jugular, near the posterior end of the "club-muscle;" 2. An anastomosis of the posterior end of the anterior cardinal with the portal system; 3. An obliteration of the primitive anterior cardinal vessel *just behind* each of these anastomoses. Furthermore, by a union of the anterior ends of the posterior common cardinals, the blood was diverted from the *right* into the left *ductus* Cuvieri, and the right ductus disappeared entirely. The embryology of the cardinal veins, when worked out, will decide whether this is the true explanation of the present condition in *Bdellostoma*.

In no other fishes does the blood from the walls of the anterior body region pass into the portal system. It is said

to occur in some Testudinata and Amphibia, however. The portal system of *Bdellostoma* is also remarkable in being developed chiefly from the supra-intestinal vein, and in having no connection whatever with the sub-intestinal vein.

A well developed portal heart, contractile and supplied with a complete system of valves, so far as I know, occurs nowhere else among Vertebrates (excepting the closely related *Myxine*?). Contractile veins, however, are not uncommon.

I may sum up my conclusions in regard to the Comparative Anatomy as follows:

PRIMITIVE CHARACTERS IN THE BLOOD-VASCULAR  
SYSTEM OF BDELLOSTOMA.

1. Persistent pericardio-peritoneal foramen.
2. The simple tubular heart.
3. The large number (up to 14) of functional branchial vessels.
4. The origin of the carotid arteries from a lateral commissural vessel on each side connecting all the efferent branchial arteries.
5. The complete sub-chordal aorta (dorsal aorta) extending forward into the head region.
6. Segmental arrangement of the somatic and renal arteries and veins.
7. Frequent anastomosis between the posterior cardinal veins.
8. Persistent sub-intestinal vein which does not join the portal system.
9. The presence of an inferior jugular vein.
10. The contractility of the portal heart.

CHARACTERS SECONDARILY ACQUIRED.

1. The asymmetry of the venous system.
2. Distribution of branchial vessels to gill slits instead of gill arches.
3. The extension of the portal system into the territory of the right anterior cardinal vein.

4. The connection of the caudal vein with the posterior cardinals.
5. The presence of a well developed valvular portal heart.

## EXPLANATION OF LETTERING USED IN FIGURES.

|                                                           |                                                             |
|-----------------------------------------------------------|-------------------------------------------------------------|
| <i>A</i> , . . . auricle.                                 | <i>dcd</i> , . . . deep anterior cardinal.                  |
| <i>Al</i> , . . . alimentary canal.                       | <i>ep</i> , . . . epithelium of the gill cavity.            |
| <i>Av</i> , . . . ventral aorta.                          | <i>ef. br</i> , . . . efferent branchial artery.            |
| <i>Aa</i> , . . . anterior dorsal aorta.                  | <i>ext. car</i> , external carotid artery.                  |
| <i>Ap</i> , . . . posterior dorsal aorta.                 | <i>gen</i> , . . . genital branches.                        |
| <i>BA</i> , . . . bulbus aortæ.                           | <i>gb</i> , . . . gall cyst.                                |
| <i>Car</i> , . . . right common carotid.                  | <i>gpc</i> , . . . external gill passage.                   |
| <i>Cal</i> , . . . left common carotid.                   | <i>gpi</i> , . . . internal gill passage.                   |
| <i>H</i> , . . . portal heart.                            | <i>gp</i> , . . . cavity of the gill pouch.                 |
| <i>I</i> , . . . intestine.                               | <i>g</i> , . . . gill pouch.                                |
| <i>L</i> , . . . liver.                                   | <i>ha</i> , . . . anterior hepatic vein.                    |
| <i>La</i> , . . . anterior lobe of the liver.             | <i>hp</i> , . . . posterior hepatic vein.                   |
| <i>Lp</i> , . . . posterior lobe of the liver.            | <i>i</i> , . . . inner (visceral) layer of the pericardium. |
| <i>M</i> , . . . mesentery.                               | <i>ic</i> , . . . "intercostal" vessel.                     |
| <i>S</i> , . . . sinus venosus.                           | <i>int. car</i> , internal carotid artery.                  |
| <i>T</i> , . . . lobules of testis.                       | <i>jv</i> , . . . inferior jugular vein.                    |
| <i>V</i> , . . . ventricle.                               | <i>lbr</i> , . . . lateral branch.                          |
| <i>aha</i> , . . . anterior hepatic artery.               | <i>mc</i> , . . . mesocardium.                              |
| <i>acl</i> , . . . left anterior cardinal vein.           | <i>mnr</i> , . . . right mesonephros.                       |
| <i>acr</i> , . . . right anterior cardinal vein.          | <i>mnl</i> , . . . left mesonephros.                        |
| <i>avv</i> , . . . auriculo-ventricular valves.           | <i>mw</i> , . . . muscular wall of gill pouch.              |
| <i>av</i> , . . . aortic valves.                          | <i>my</i> , . . . myotomes.                                 |
| <i>af. br</i> , . . . afferent branchial arteries.        | <i>mes</i> , . . . mesenteric arteries.                     |
| <i>ap</i> , . . . anterior portal vein.                   | <i>ntc</i> , . . . notochord.                               |
| <i>cv</i> , . . . cystic vein.                            | <i>o</i> , . . . outer (parietal) layer of the pericardium. |
| <i>cm</i> , . . . "club-muscle."                          | <i>ocd</i> , . . . oesophago-cutaneous duct                 |
| <i>clb</i> , . . . "club-muscle" branches.                | <i>pcr</i> , . . . right posterior cardinal vein.           |
| <i>cap</i> , . . . capillary network.                     | <i>pcl</i> , . . . left posterior cardinal vein             |
| <i>conv</i> , . . . connecting vessel.                    | <i>pcc</i> , . . . common posterior cardinal                |
| <i>cpa</i> , . . . anterior branch of the common portal.  | <i>ph</i> , . . . pharyngeal branches.                      |
| <i>cpp</i> , . . . posterior branch of the common portal. | <i>pnr</i> , . . . right pronephros.                        |
| <i>coel</i> , . . . coeliac artery.                       | <i>pnl</i> , . . . left pronephros.                         |
| <i>caud</i> , . . . caudal vessel.                        | <i>ptc</i> , . . . peritoneal cavity.                       |
| <i>cp</i> , . . . common portal vein.                     | <i>pcf</i> , . . . pericardio-peritoneal foramen.           |
| <i>d</i> , . . . dermal branches.                         |                                                             |



|                                                        |                                           |
|--------------------------------------------------------|-------------------------------------------|
| <i>pcv</i> , . . . pericardial cavity.                 | <i>supr.int</i> , supra-intestinal vein.  |
| <i>pha</i> , . . . posterior hepatic artery.           | <i>sn</i> , . . . "intercostal" nerve.    |
| <i>rbc</i> , . . . red blood corpuscles.               | <i>sgl</i> , . . . slime glands.          |
| <i>r</i> , . . . renal branches.                       | <i>sav</i> , . . . sinu-auricular valves. |
| <i>spc</i> , . . . spinal cord.                        | <i>s</i> , . . . somatic vessels.         |
| <i>sub.int</i> , sub-intestinal vein.                  | <i>vv</i> , . . . valves of portal heart. |
| <i>scd</i> , . . . superficial anterior car-<br>dinal. | <i>vg</i> , . . . vagus nerve.            |
|                                                        | <i>x</i> , . . . "ductus Botalli,"        |

In figures IV, V, VI, red line indicates peritoneum; in all other figures—red, arteries; blue, veins; green, portal vessels.

#### EXPLANATION OF PLATES.

Plate I includes Figures I-IX.

Plate II includes Figures X-XVI.

Plate III includes Figures XVII-XX.

FIGURE I.—Heart of *Bdellostoma dombeyi* ( $\times 1$ ). Dorsal view.

A, auricle. V, ventricle. S, sinus venosus. BA, bulbus aortæ. jv, inferior jugular vein. acl, left anterior cardinal. pcc, posterior common cardinal. ha, anterior hepatic vein. hp, posterior hepatic vein.

FIGURE II.—Heart of *Bdellostoma dombeyi* ( $\times 1$ ). Ventral view. Lettering same as in Fig. I.

FIGURE III.—Heart of *Bdellostoma dombeyi* ( $\times 2$ ). Showing a dorsal view of the ventral half of the auricle and ventricle, the dorsal half having been removed by a horizontal section.

sav, sinu-auricular valves. avv, auriculo-ventricular valves. av, aorta valves. Otherwise as in Fig. I.

FIGURE IV.—Diagram of cross section passing through the mid-abdominal region of *Bdellostoma*.

M, mesentery. A, alimentary canal. ptc, peritoneal cavity.

FIGURE V.—Diagram of cross section passing through the posterior lobe of the liver in *Bdellostoma*.

L, liver.

FIGURE VI.—Diagram of cross section passing through the ventricle and anterior lobe of the liver. Showing the relation of the pericardial cavity to the general peritoneal cavity.

pcf, pericardio-peritoneal foramen. pcv, pericardial cavity. o, outer or parietal layer of the pericardium. i, inner, or visceral pericardial layer. me, mesocardium. V, ventricle. Dotted line, pericardium.

FIGURE VII.—Testis of *Bdellostoma dombeyi* ( $\times 2$ ), showing the arterial supply. The genital fold lies on the right side of the mesentery.

wS, mesenteric artery. qs, genital branches. T, lobules of testis. Ap, posterior dorsal aorta.

FIGURES VIII AND XIV.—Highly magnified portions of the smallest branches of a gill leaflet ( $\times 450$ ).

cap, capillary wall. ep, epithelium lining gill cavity. rbc, red blood corpuscles. con, connective tissue.

FIGURE IX.—Cross section of an injected gill pouch of *Bdellostoma* ( $\times 8$ ). Taken perpendicular to the gill axis, about at the center.

Camera lucida outline.

mw, muscular wall of gill pouch. gp, cavity of gill, into which gill leaflets project.

FIGURE X.—Branchial region of *Bdellostoma dombeyi* ( $\times 1\frac{1}{2}$ ). Ventral view. Body wall opened by a median longitudinal incision, and the lateral flaps folded back. Anterior lobe of the liver removed to expose heart. Arteries colored red. Veins blue.

Av, ventral aorta. af. br, afferent branchial arteries. x, on last afferent branchial artery indicates position of "ductus Botalli." ic, "intercostals" (arteries red, veins blue). S, Sinus venosus. jv, inferior jugular vein. acl, left anterior cardinal vein. supr. int, supra-intestinal vein. A, auricle. V, Ventricle. H, portal heart. Lp, posterior lobe of liver. gb, gall bladder. mnr, mnl, right and left mesonephros. pnr, pnl, right and left pronephros. pcf, pericardio-peritoneal foramen (dotted outline). sgl, slime glands. ocd, oesophago-cutaneous duct. cm, "club-muscle." gpe, spe, external gill passages.

FIGURE XI.—Lateral view of the viscera of *Bdellostoma dombeyi* left side, including ventral view of the left half of the body wall, which has been laid back ( $\times 1$ ).

cpa, anterior branch of common portal vein. cpp, posterior branch of common portal vein. Jv, inferior jugular vein. acl, left anterior cardinal. ha, hp, anterior and posterior hepatic veins. cpa, cpp, anterior and posterior branches of common portal vein. ocl, left posterior cardinal. supr. int, supra-intestinal vein. sub. int, sub-intestinal vein. La, Lp, anterior and posterior lobes of the liver. pnl, left pronephros. mnl, left mesonephros. ic, "intercostal" vessels. Otherwise as previously.

FIGURE XII.—Mid abdominal region of *Bdellostoma dombeyi*, showing ventral view of the left side of the body wall, and a lateral view of the intestine and mesentery. The latter have been laid over upon the right side of the body wall, and the mesentery stretched out ( $\times 2$ ).

r, renal branches. s, somatic branches (red, arteries; blue, veins). pcl, pcr, posterior cardinal veins, left and right. mes, mesenteric arteries. vg, vagus nerve. sn, "intercostal" nerve. Otherwise as previously.

FIGURE XIII.—Diagram of one half of a section through the gill pouch of *Bdellostoma*, parallel with the axis of the gill. Afferent vessels red. Efferent vessels blue.

af. br, afferent branchial vessel. ef. br, efferent branchial. cap, capillary network.

FIGURE XIV.—See Fig. VIII.

FIGURE XV.—Diagram of a cross section through the body of *Bdellostoma*, just behind the liver.

ntc, notochord. spc, spinal cord. s, somatic branches. ic, "intercostals." d, dermal branches. my, myotomes. Otherwise as previously.

FIGURE XVI.—A ventral view of the dorsal wall of the portal heart of *Bdellostoma dombeiyi*, the ventral half having been cut away. ( $\times 2$ .)

ap, anterior portal vein. supr. int, supra-intestinal vein. cp, common portal vein. vv, valves.

FIGURE XVII.—Diagram of the venous system of *Bdellostoma*, dorsal view (approximately natural size). Portal system, green; general system blue. On the right side, the renal branches of the posterior cardinal are omitted. On the left side, the somatic branches are omitted.

acr, acl, right and left anterior cardinals (or jugulars). dcd, scd, deep and superficial branches of anterior cardinals. s, somatic veins. ph, pharyngeal branches. clb, "club-muscle" branches. jv, inferior jugular vein. S, sinus venosus. pnl, pnr, left and right pronephros. pcc, posterior common cardinal. pcr, pcl, right and left posterior cardinals. ha, hp, anterior and posterior hepatic veins. caud, caudal vein. ap, anterior portal vein. cp, common portal vein. gb, gall bladder. sub. int, sub-intestinal vein. gen, genital veins.

FIGURE XVIII.—Diagram of entire circulatory system in *Bdellostoma* lateral view (approximately natural size). Arterial system, red; general venous system, blue; portal system, green.

Lettering same as Figs. XVII and XX.

FIGURE XIX.—Lateral view of the viscera of the pharyngeal and cardiac regions, including ventral view of the right side of the body wall ( $\times 1\frac{1}{2}$ ). In this figure the viscera have been laid over upon the left side, in order to show the relation of the blood vessels to the body wall. As a result, the somatic branches of the anterior portal and dorsal aorta in the branchial region are stretched somewhat beyond their normal length.

Aa, anterior dorsal aorta. Ap, posterior dorsal aorta. Car, right common carotid. pb, pharyngeal branches. ap, anterior portal vein. ic, intercostals. supr. int, supra-intestinal vein. cv, cystic vein. sub. int, sub-intestinal vein. pcr, right posterior cardinal. ef. br, efferent branchial vessels. clb, "club-muscle" branches.

Otherwise as previously.

FIGURE XX.—Diagram of the arterial system of *Bdellostoma dombeiyi* dorsal view (approximately natural size). The afferent branchial system is omitted. Of the branches of the posterior dorsal aorta, on the right side, the renal branches are omitted. The genital branches should be represented on the right side.

V, vertebralis impar. lbr, lateral branch. ext. car, int. car, external and internal carotid arteries. s, somatic arteries. Car, Cal, right and left common carotid arteries. ef. br, efferent branchials. con. v. connecting vessels. coel, coeliac artery. caud, caudal artery. ren, renal branches. mes, mesenteric arteries.



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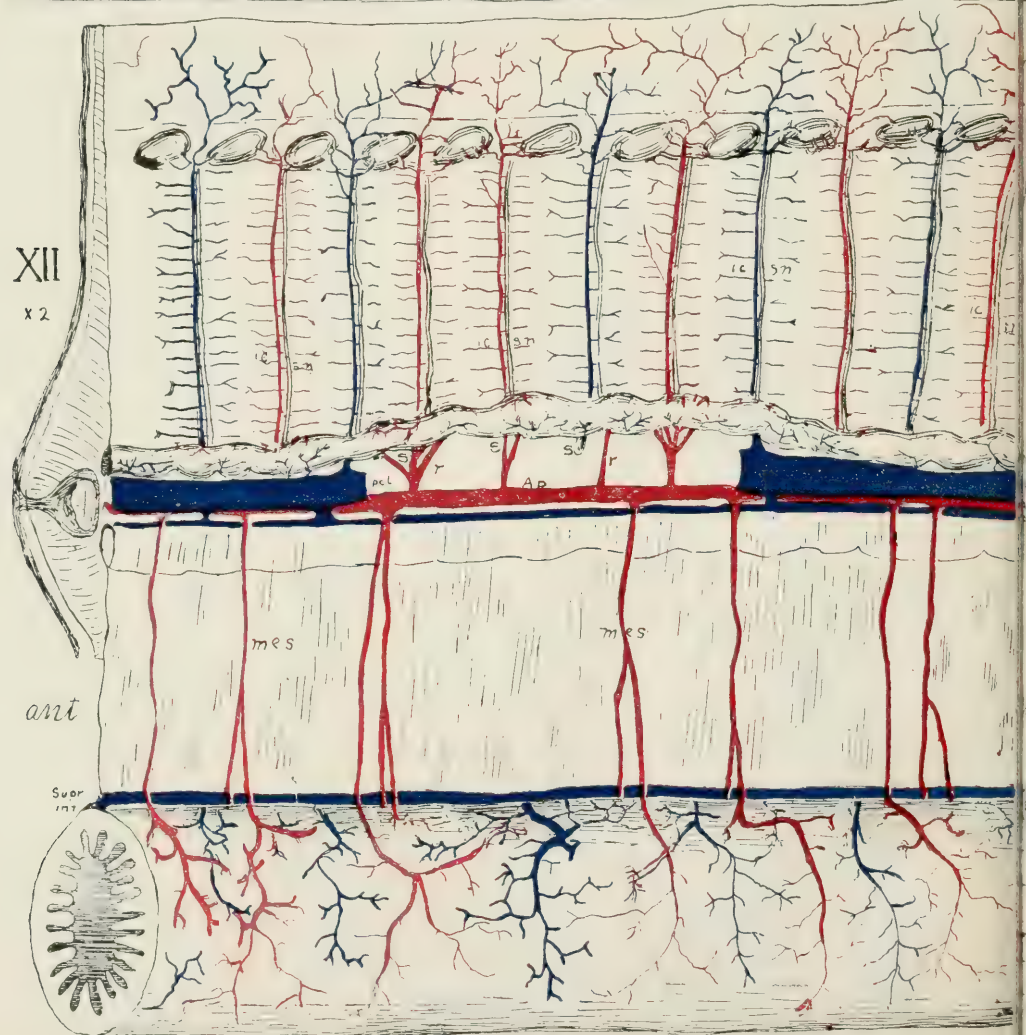
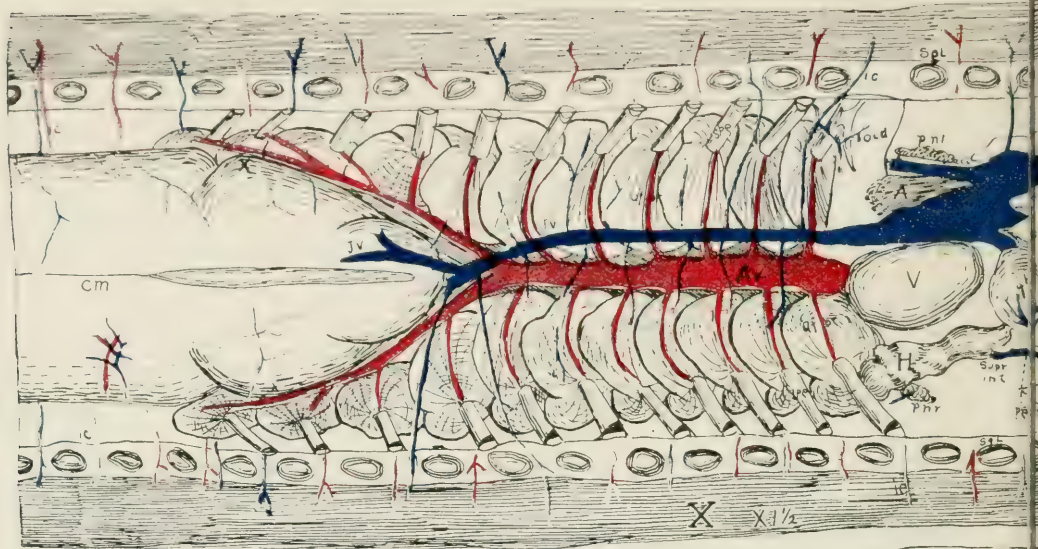
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C. M. JACKSON, Vascular System of *Bdellostoma dombeyi*.

